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The colourful journey of the Eurasian Collared Dove *Streptopelia decaocto*

by Hein van Grouw

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Summary.—In the 18th and 19th centuries the Eurasian Collared Dove *Streptopelia decaocto* was widely considered to be the wild ancestor of the domesticated Barbary Dove (domestic *S. risoria*), and even following its recognition as a species its taxonomic status was a source of confusion. Since 1900, and the species' massive geographic expansion (both naturally and by introduction) the two taxa have occasionally met. The resultant hybridisation is probably the cause of the large number of Eurasian Collared Doves with the aberrant pale colour of Barbary Doves in areas where hybridisation has occurred.

'*Besides variation in depth of colour within the normal range, very pale individuals and others that are creamy buff like* S. 'risoria' *occur quite frequently in Britain. There is no reason to suppose these mutants are of hybrid origin*'. Goodwin (1983: 116)

Even before the first Eurasian Collared Doves *Streptopelia decaocto* were officially recorded in the British Isles, James Fisher (1953) detailed the species' spread across Europe. Subsequently, under their own steam they have reached continental Africa and, with a little human help, they have also become common in the USA. Prior to the mid 1800s, Eurasian Collared Dove caused taxonomic confusion among ornithologists, and since 1900 it has generated interest due to its spectacular range expansion. Nowadays, many consider the species an annoyance, or at least unworthy of attention, but given its remarkable—even colourful—natural history, Eurasian Collared Dove surely deserves greater appreciation.

Frivaldszky (1838), a naturalist at the Budapest museum, was first to describe Eurasian Collared Dove taxonomically and gave it, based on legend, the species name *decaocto* (Appendix 1). Although the message the dove was supposed to pronounce—deca-octo—may not be immediately obvious (try matching this two-syllable word with the three-syllable call, see Appendix 1), Eurasian Collared Dove has certainly succeeded in proclaiming it widely across the world. Its original distribution was South Asia, but by 1800 the species was already common in Central Asia, the Balkans and European Turkey (Stresemann & Nowak 1958, Nowak 1965). Since the early 20th century it has continued to expand west and south across Europe (Nowak 1965) and, around 1986, it 'jumped' from Spain to continental Africa (Robel 2000). Roughly 12 years earlier Eurasian Collared Dove was introduced in North America where it has continued to expand. It is in North America, 'the land of opportunity', where the Eurasian Collared Dove may eventually evolve into a new taxon...

Confusing taxonomy

Although described taxonomically in 1838 by Frivaldszky based on birds from the Balkans, it took another 100 years or more before Eurasian Collared Dove became familiar in the rest of Europe. It was unknown in Western Europe until the second half of the 20th

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century, thus its call sounding in the background of many films and dramas set in pre-WWII Europe is an often-unnoticed inaccuracy!

During his travels through Hungary, Johann Friederich Naumann (1780–1857) met Frivaldszky in Budapest, who showed him turtle dove skins in the museum's collection, collected in 1835 in Plovdiv, Bulgaria (formerly Philippopolis, European Turkey). Eurasian Collared Dove, then still referred to as Indian Turtle Dove *Columba risoria*, was generally considered to be the wild form of the domesticated Barbary Dove[1], which was the only 'collared turtle-dove' known in Europe at the time. Naumann, however, correctly recognised the skins as different from the domestic dove and was keen to investigate further. He therefore returned to Germany with three of the skins, which he sent to M. H. C. Lichtenstein in Berlin to compare with other specimens collected in Asia and Africa. Lichtenstein, however, believed that different climates result in variety within a species, an idea introduced by C. L. Gloger in 1833 (Gloger's Rule; animals tend to be darker in warm and humid areas). Having compared Frivaldszky's birds with similar doves from elsewhere, which he considered to all be *risoria*[2], Lichtenstein believed the Bulgarian doves were not significantly different and therefore not a new species (Stresemann 1953).

Based on these two rather different conclusions, Frivaldszky (1838) named the Eurasian Collared Dove *Columba risoria* var. *decaocto* (descriptions of varieties from this era can represent valid species-group names). The original description was published in Hungarian, and, as the journal was rather obscure, Frivaldszky's name *decaocto* for Eurasian Collared Dove was long overlooked. As Naumann had encouraged him to describe the species, and also produced its accompanying plate (Fig. 1), Frivaldszky gifted him a specimen (Figs. 2–3).

Brian Houghton Hodgson (1801–94), Britain's diplomatic representative in Nepal between 1820 and 1843, amassed a large collection of birds and mammals. When he returned to England in 1843, he donated this collection, including *c*.2,200 bird skins, to the British Museum, and it still is one of the most important of its kind from the Himalayan region. His collection was augmented by drawings commissioned from native artists depicting each species, each drawing numbered and cross-referenced to a specimen label attached to the leg or neck of the skin (Fig. 4). Nearly the complete set of drawings was donated to the museum with the specimens (Gray 1844). Hodgson's intentions in compiling this visual catalogue are unclear. He may have planned to use them for a publication about the birds of Nepal, although there appears to be no direct evidence for this.

Among the Nepalese birds in Hodgson's collection are several specimens of Eurasian Collared Dove, which he labelled no. 107 in line with the species' numbered drawing (Fig. 5). He had also sent to the museum a list of the species he had collected, which was published in *The zoological miscellany* (Hodgson 1844). Therein, Hodgson referred to the species as *Columba douraca* (presumably from its Hindi name, 'Dhor fakhta'[3]). The name *douraca* was never published formally by Hodgson and is not mentioned on the drawing, so

[1] Barbary Dove is the domestic form of African Collared Dove *Streptopelia risoria*. Until the late 1800s, however, many ornithologists considered Eurasian Collared Dove, which they called *Columba* (*Streptopelia*) *risoria*, to be the wild ancestor of Barbary Dove (van Grouw 2018).

[2] The different specimens Lichtenstein used in his comparison, and whose differences he believed were the result of climate, belonged to five different species (Stresemann 1953); African Collared Dove, Barbary Dove, Vinaceous Dove *S. vinacea*, Ringed Dove *S. capicola*, Mourning Collared Dove *S. decipiens* and Eurasian Collared Dove.

[3] Newman (1906) assumed that Hodgson's name *douraca* was founded on a bird from a place called Dhourakha, which he presumed was in Nepal, but admitted that he could not find it on a map.

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Figure 1. Depiction by J. F. Naumann of Eurasian Collared Dove *Streptopelia decaocto* to accompany the species' type description by Frivaldszky in 1838 (Hein van Grouw, © Natural History Museum, London)

Figure 2. Type specimen of *Streptopelia decaocto*, collected in 1835 in Plovdiv, Bulgaria by Carl Hinke, in the Naumann Museum, Köthen (© Naumann Museum, Köthen)

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Figure 3. Watercolour by J. F. Naumann of the type of *Streptopelia decaocto*, previously published only in the Naumann Museum guidebook (© Naumann Museum, Köthen)

is a *nomen nudum*[4]. Nevertheless, it was accepted by many authorities as the species name of Eurasian Collared Dove (Fig. 6), e.g., Schlegel (1873), Stejneger (1887) and Salvadori (1893). These, and many other contemporary authors, no longer considered the species to be the wild ancestor of the domestic Barbary Dove.

However, Othmar Reiser, an Austrian ornithologist and curator at the National Museum of Bosnia and Herzegovina in Sarajevo, discovered Frivaldszky's work and realised that the specific name *decaocto* antedates Hodgson's *douraca*. He published that the correct name for Eurasian Collared Dove is *decaocto*, firstly in German (1894), and later, via Dresser (1903) in English. After Hodgson more workers had named the species, but all of these names are junior synonyms of *decaocto* (see Appendix 2).

As mentioned, Eurasian Collared Dove was long known mainly by the name *risoria*, and later *douraca*, from India. Indian birds are generally smaller and darker than those

[4] *Nomen nudum* ('naked name') is a nomen that seems to be a correct scientific name, and may originally have been intended to be one, but which has not (yet) been published with an adequate description of the taxon involved and therefore cannot be accepted under the *International code of zoological nomenclature*.

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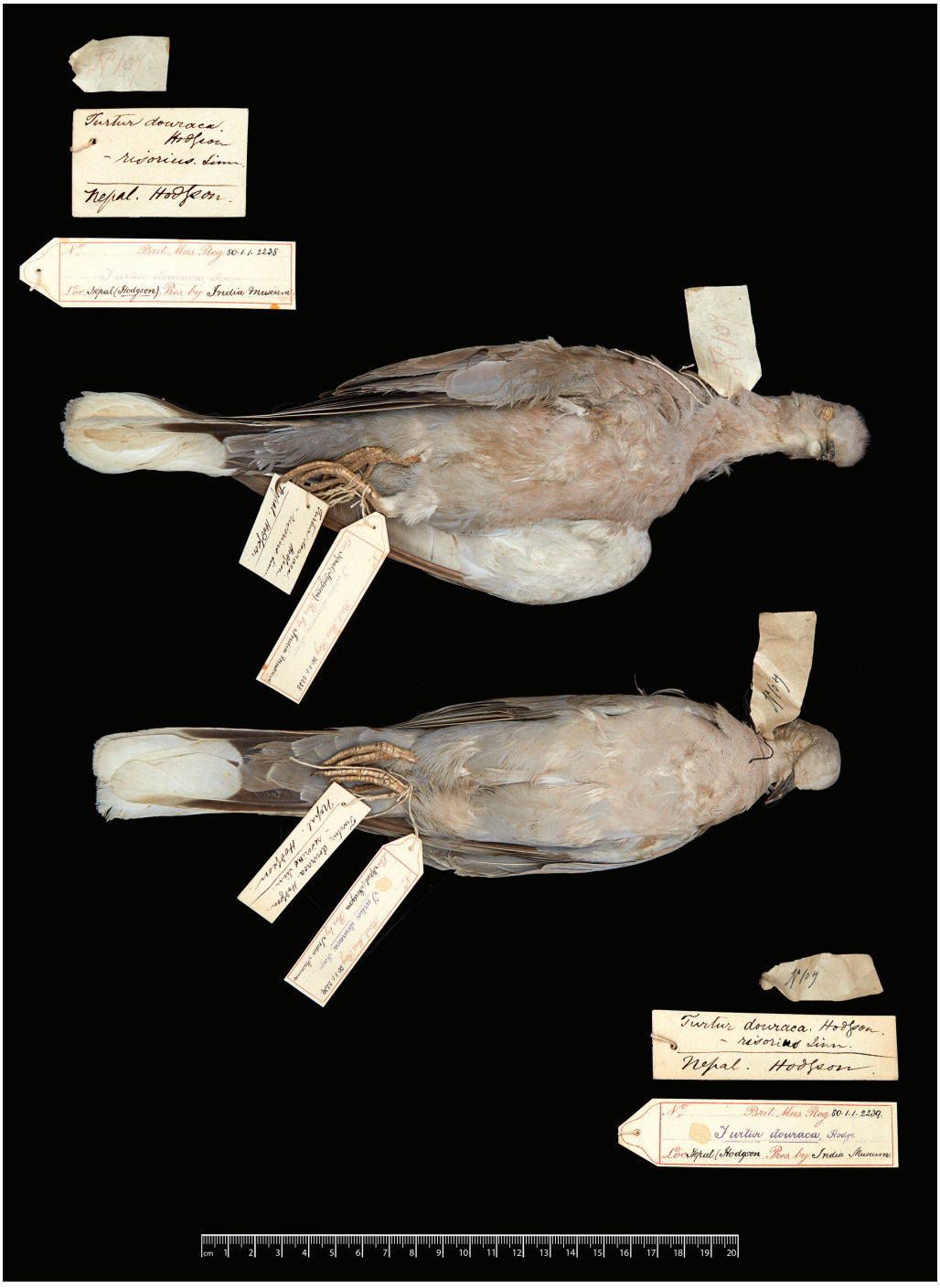

Figure 4. Eurasian Collared Dove *Streptopelia decaocto* specimens collected by Hodgson in Nepal, and which he called *Columba douraca*. His collection was augmented by a set of drawings depicting each species, commissioned from native artists, numbered and cross-referenced to a label attached to the specimens. The drawing of *Columba douraca* is no. 107. Specimens NHMUK 1880.1.1.2238 and NHMUK 1880.1.1.2239, Natural History Museum, Tring (© Aimee McArdle, Natural History Museum, London)

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Figure 5. Drawing no. 107; Hodgson's *Columba douraca* from Nepal (© Natural History Museum, London)

Figure 6. Despite the specific name *douraca* never being published by Hodgson, it was nevertheless accepted by many ornithologists as the name for Eurasian Collared Dove and specimens were labelled accordingly, including this Eurasian Collared Dove collected in the 1820s in Japan by P. F. von Siebold, in the Naturalis Biodiversity Center, Leiden, RMNH.AVES.258559 (© Naturalis Biodiversity Center, Leiden)

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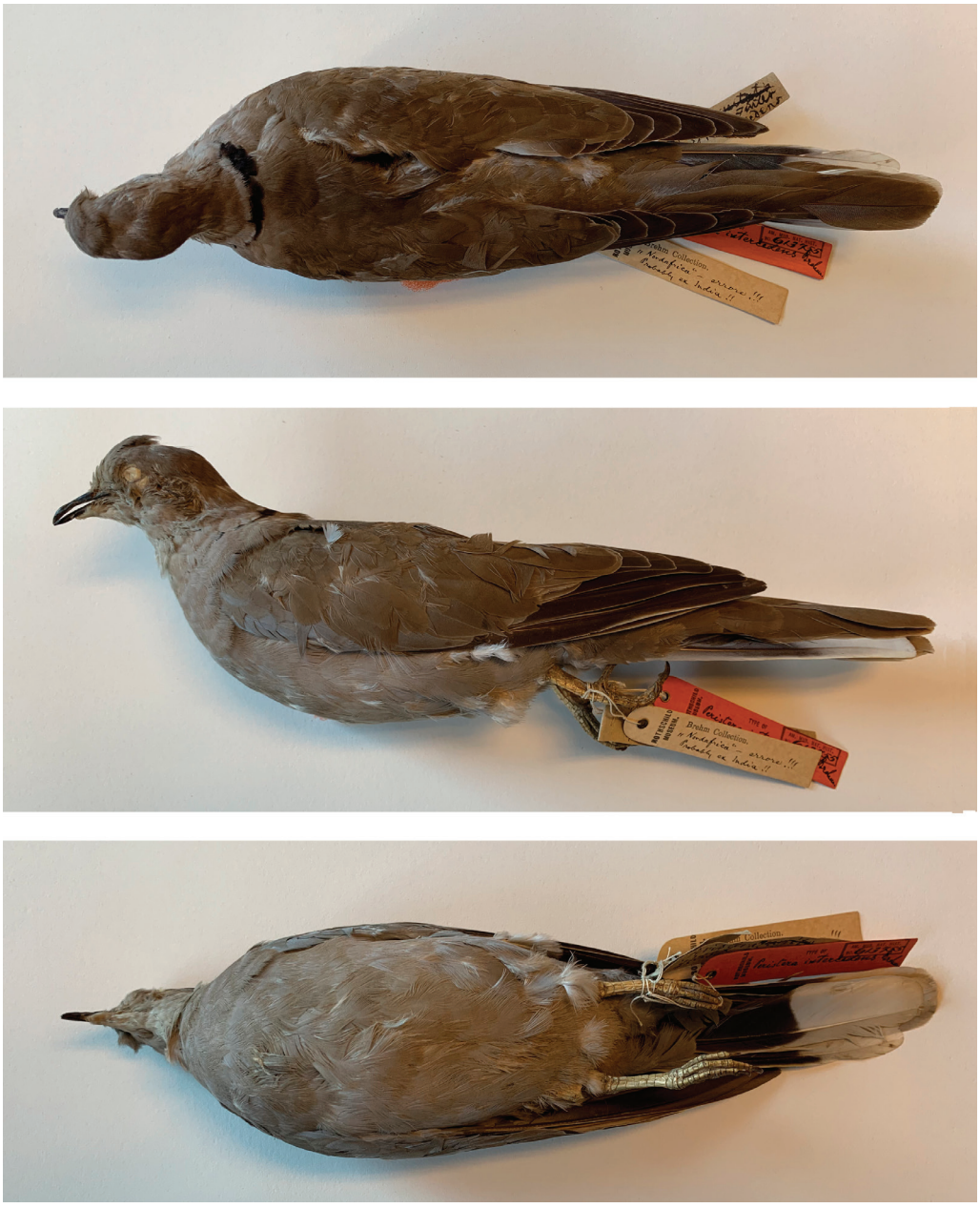

Figure 7. Type specimen of *Peristera intercedens*, AMNH 613755; Brehm (1855) incorrectly thought it came from Africa but, based on its dark colour and small size, it almost certainly was collected in southern India or Sri Lanka (© American Museum of Natural History, New York)

in the Balkans and Central Asia. Newman (1906) therefore suggested recognising them as different subspecies: the larger and paler birds, after Frivaldszky's Balkan doves, *S. d. decaocto*, and the darker smaller birds from India as *S. d. douraca*, after Hodgson's doves from Nepal. This, however, was never accepted. In fact, if there had been the need to distinguish these two, Brehm's name *intercedens* is the earliest available name for Indian birds. Based on a Eurasian Collared Dove specimen from his own collection (Fig. 7), Brehm

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Figure 8. Eurasian Collared Dove *Streptopelia decaocto xanthocyclus*, Bagan, Myanmar, 15 November 2013 (© Otto Samwald)

(1855) named the species *Peristera intercedens*, the Middle Laughing Dove[5]. From where and whom he obtained the specimen are unknown, but Brehm assumed incorrectly that it was from North Africa. Based on its small size and dark colour the specimen was almost certainly from (southern) India or Sri Lanka.

Currently all populations in Europe and Asia, except Myanmar (see below), are considered *decaocto*. The difference in size is often explained by Bergmann's Rule (Keve-Kleiner 1943, Nowak 1975), an ecogeographical rule which states that within a broadly distributed taxonomic group, populations in colder environments are larger than those in warmer regions. Although originally formulated in the context of species within a genus, it has often been recast in terms of populations of a species, as may be the case for Eurasian Collared Dove. Doves from South India and Sri Lanka are indeed smallest, but also generally darkest in colour, which, however, cannot be explained by Bergmann's Rule, but rather by Gloger's Rule.

The doves in Myanmar, however, are more distinctive and easily recognised from those in Europe and elsewhere in Asia. Besides being slightly darker overall, they have a distinctive yellow orbital ring instead of greyish white (Fig. 8). Although Oates (1883: 293) already mentioned this characteristic ('eyelids and skin of face yellow'), prior to the early 20th century no one else had drawn attention to the fact that Burmese birds differed in this respect from Indian ones. It was Newman (1906) who fully recognised this difference, based on a live bird in London Zoological Gardens, which he described as a new subspecies, *xanthocyclus*, for its yellow orbital ring. In fact, in October 1896 the zoo had received three individuals, presumably from the Minbu and Mague districts of upper Burma. One, a male,

[5] In many languages, including German, Barbary Dove is called 'Laughing Dove' (Lachtaube) for the typical laughing call it makes when excited (in contrast, Laughing Dove *Streptopelia senegalensis* does not give a laughing call at all!). In the past, similar-looking species with a black neck-ring were often also referred to as 'laughing dove'. Brehm (1855) distinguished six different 'species' of 'Lachtaube', including domestic Barbary Dove, African Collared Dove, Eurasian Collared Dove, Vinaceous Dove *S. vinacea*, Red-eyed Dove *S. semitorquata* and Dusky Turtle Dove *S. lugens*.

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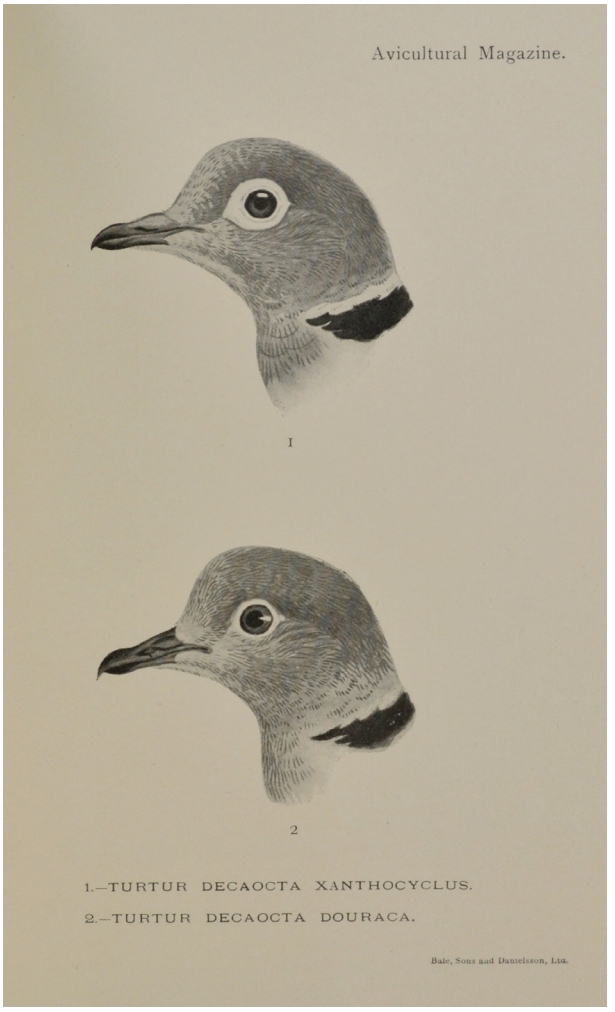

Figure 9. Illustration in Newman (1906) captioned 'Fig 1. Head of *Turtur decaocto xanthocyclus*, from the original sketch of the living bird [whereabouts of the original sketch unknown]. Fig. 2. Head of *Turtur decaocto douraca*, traced from the Indian drawing in Hodgson's MSS. Birds of India, Vol. V., pl. 82, type of *Turtur douraca*' (Hein van Grouw, © Natural History Museum, London)

lived almost ten years in the zoo but when, around 1904, Newman's attention was drawn to this dove, the other two had already died. Unfortunately, despite Newman's request, the dove's skin was not retained as, apparently, the cadaver was heavily damaged by rats post-mortem (Newman 1906), so the type specimen of *xanthocyclus* no longer exists (Fig. 9).

Currently only two subspecies of Eurasian Collared Dove are recognised—*decaocto* and *xanthocyclus*—and birds introduced to the Americas are of the nominate race.

Global spread—a brief overview

The original range of Eurasian Collared Dove is assumed to have been arid areas in South Asia (Stresemann & Nowak 1958, Nowak 1965). Precisely when the species started spreading into the Balkans and European Turkey is unknown, but by 1800 it was already common there (Stresemann & Nowak 1958, Nowak 1965).

In those areas of the Balkans formerly under Turkish control (i.e. part of the Ottoman Empire), e.g., parts of Bulgaria, Serbia, Albania and Herzegovina, Eurasian Collared Dove flourished in the towns and cities because it was protected mainly by the Muslim population (Matvejev 1950). They encouraged the species by providing nest sites around their houses

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(Naumann 1837, McGregor 1906), and in certain areas the punishment for killing a dove was a fortnight in prison (Reiser 1939). However, once the Turks were forced to cede their occupation of the Balkans in 1878, a large part of the Muslim population left, thus Eurasian Collared Dove lost its protector, its numbers diminished rapidly and in certain areas disappeared completely (Reiser 1894, 1939, Pichler 1906). After 1900 it made a slow recovery and by 1930 had regained its former distribution in the Balkans. Thereafter, the species appeared unstoppable and continued its expansion; in a relatively short period the rest of Europe was colonised. This spread was documented in detail by Fisher (1953), Stresemann & Nowak (1958) and Nowak (1965, 1991). As Turkey is considered the type locality of Eurasian Collared Dove, and the colonisation proceeded via Turkey into the rest of Europe, in many countries the common name refers to this (e.g., Dutch: Turkse Tortelduif, German: Türkentaube, French: Tourterelle Turque, Danish: Tyrkerduen, Swedish: Turkduva, Spanish: Tórtola Turca, Portuguese: Rola-turca). The first bird in England was recorded in summer 1952 at Manton, Lincolnshire (May & Fisher 1953), where it remained until at least 1958, but never found a mate (Hudson 1965). Close by, however, in Yorkshire, a bird dealer was known to have sold Eurasian Collared Doves imported from India between 1947 and 1951. Although no escapes were recorded, the Lincolnshire bird could have been one of the imported individuals, so it was never accepted as the first British record. Three years later, however, there was no doubt about the pair that turned up in Cromer, Norfolk, making 1955 the date of the first official record in Britain (Hudson 1965).

The species was first recorded in captivity in the USA around 1900, when 24 individuals were in the property of Charles Otis Whitman (1842–1910), Professor of Zoology at the University of Chicago. They were imported from Japan to be used in his studies on behaviour, inheritance and hybridisation in pigeons. Whitman called them the 'Japanese Ring-dove' *S. douraca* (Whitman 1919). But their fate after Whitman died in 1910 is unknown.

In all probability the origin of the Eurasian Collared Dove in America was the aviary of a bird breeder in Nassau, New Providence in the northern Bahamas. In fact, the origin was the Netherlands, which is where he obtained his birds in the early 1970s, although he thought they were Barbary Doves! In late 1974 several escaped, influencing the breeder's decision to release the remainder, and it is believed that in all 50 individuals were liberated (Smith 1987). Given the species' 'urge' to expand, and probably also due to the warm climate, they thrived and in less than ten years all the islands to the west were colonised. Probably by the late 1970s but certainly in the early 1980s, Eurasian Collared Doves were present at several places in Florida and, consistent with the usual westward direction of this species' expansion, surely arrived from the Bahamas. At the time several populations of feral Barbary Doves were flourishing in south-east Florida, so the new arrival remained unnoticed for a while, making the precise year of arrival unknown (Smith & Kale 1986).

Probably after the first doves reached Florida hybridisation with the feral Barbary Doves occurred. However, Eurasian Collared Doves, and probably their hybrids too, continued their march across the continent. Currently, the species can be found in nearly every North American state, in parts of Canada and Mexico, as well as Central America.

Colour aberrations

Compared to its close relative, the domestic form of African Collared Dove *Streptopelia risoria* (Barbary Dove), remarkably few colour aberrations are known in Eurasian Collared Dove. One, however, is rather common and occurs throughout the species' range. It is often referred to as buff, blond or leucistic, but is a form of Ino and is the same mutation

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as occurs in Barbary Dove[6] (van Grouw 2018). The Ino mutation is a variation of the gene SLC45A2 (pers. obs.; Appendix 3), which codes for a protein in the melanin cells and regulates melanin synthesis (Domyan *et al*. 2014). Several mutations of this gene, located on the sex-chromosome in birds, have been recorded in many different bird species (Appendix 3). The Ino mutation in Barbary and Eurasian Collared Doves causes incomplete melanin synthesis; the quantity of melanin granules is unchanged but the granules are lighter in colour, resulting in the overall plumage being paler, and the usually blackish and greyish parts more brownish. Due to the high concentration of melanin in the neck-ring, the change in colour in this feature is invisible to the naked eye. Although Goodwin (1973, 1983) believed the mutation occurred naturally in the species and not as a result of hybridisation with Barbary Dove, some facts could suggest otherwise. For example, the Canary Islands already had an established population of feral Ino-coloured Barbary Doves before the Eurasian species arrived around 1989, colonising all islands in the archipelago within ten years (Garcia-del-Rey 2015). Barbary Dove still breeds locally on all islands except El Hierro (Bowler 2018) but numbers have declined, presumably due to being outcompeted by the larger and more aggressive Eurasian Collared Dove. The two species did hybridise on the islands (pers. obs.), which suggests a role for inter-species hybridisation in generating this colour aberration in Eurasian Collared Dove. The number of pale-coloured (Ino) Eurasian Collared Doves on the Canaries is certainly very high (Figs. 10–13).

Ino individuals recorded in countries with no established feral Barbary Dove populations (Figs. 14–16) may indeed be the result of recurrent mutation or ancestral variation in the Eurasian species. For example, an Ino-coloured fledgling found in the Netherlands, rescued and kept in captivity, aside from its colour, showed no morphological or behavioural signs of recent hybridisation (see footnote 6). However, it cannot be ruled out that the trait originated from an early hybridisation event with Barbary Dove. Knowingly or unknowingly, hybrids are bred in captivity and, when escaped or released, can survive well in the wild and interbreed with pure Eurasian Collared Doves. It is known that around 1950 Eurasian Collared Doves were imported from India into Britain by dealers (Hudson 1965), and little imagination is needed to predict that at least some of those procured by aviculturists were mated with Barbary Doves to produce hybrids. Some may have escaped or been released. The fact is Ino Eurasian Collared Doves have been observed over the last 70 years in Britain (Goodwin 1973; Fig. 17).

Barbary Doves escaping captivity in spring or summer in western Europe often survive for months or even longer, and can interbreed with the Eurasian species. Just one

[6] I conducted unpublished research into behaviour, vocalisations and colour inheritance in Barbary Dove, Eurasian Collared Dove and their hybrids for >15 years (1990–2006). One bird was a female Eurasian Collared Dove with a colour similar to Ino in Barbary Dove. Found as fledgling in the wild, other than colour the individual possessed all of the morphological and behavioural characteristics of Eurasian Collared Dove (e.g. size, mass, eye colour, tail markings and call, which are all different from Barbary Dove). The female was crossed with an Ino male Barbary Dove. All of the offspring, of both sexes, were Ino-coloured. Also, further crosses (first-generation hybrids [F1] together and F1 with both parents) produced only Ino-coloured offspring. Whether the mutation of this female Eurasian Collared Dove originated from earlier hybridisation with Ino Barbary Dove or occurred spontaneously is unclear but, based on the breeding results, it appears to be the same as Ino in Barbary Dove. In crosses and back-crosses with normal-coloured Eurasian Collared Doves, colour inheritance of this Ino Eurasian Collared Dove matched Ino in Barbary Dove (in accordance with the gene being located on the Z-chromosome; among bird breeders referred to as 'sex-linked inheritance'). In another experiment, Ino Barbary Doves (both sexes) were crossed with normal-coloured Eurasian Collared Doves, and the offspring (both sexes) successively back-crossed with Eurasian Collared Doves. Depending on which species was the male and female parent in the initial cross, after 3–5 generations of back-crossing, the Ino offspring were, in all characteristics other than colour, indistinguishable from Eurasian Collared Dove. Ino-coloured doves were identical to the Ino-coloured female Eurasian Collared Dove found as a fledgling in the wild. The normal-coloured offspring could not be distinguished from normal Eurasian Collared Doves.

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Figure 10. Ino Eurasian Collared Dove *Streptopelia decaocto*, female, La Gomera, Canary Islands, March 2010; old and heavily bleached plumage (© Alois van Mingeroet)

Figure 11. Ino Eurasian Collared Dove *Streptopelia decaocto*, male, La Gomera, Canary Islands, March 2012; old and heavily bleached plumage (© Alois van Mingeroet)

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Figure 12. Ino Eurasian Collared Dove *Streptopelia decaocto*, female, La Gomera, Canary Islands, April 2013; old and heavily bleached plumage (© Alois van Mingeroet)

Figure 13. Ino Eurasian Collared Dove *Streptopelia decaocto*, female, Lanzarote, Canary Islands, February 2018; old and heavily bleached plumage (© Nico van Wijk)

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Figure 14. Ino Eurasian Collared Dove *Streptopelia decaocto*, female, Jodhpur, Rajasthan, India, March 2013; old and heavily bleached plumage (© Pranjal J. Saikia)

Figure 15. Ino Eurasian Collared Dove *Streptopelia decaocto*, female, Tórshavn, Faroe Islands, 28 May 2020; old and heavily bleached plumage. The species is rare on the islands with just ten breeding pairs (Jens-Kjeld Jensen *in litt*. 2020), so if this female and any subsequent male offspring breed, then the mutation could become established, just as leucistic Common Ravens *Corvus corax* did in the past (van Grouw 2014) (© Marita Gulklett)

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Figure 16. Ino Eurasian Collared Dove *Streptopelia decaocto*, female, Enkhuizen, Noord Holland, the Netherlands, May 2011; old plumage bleached but fresh tertials show the colour caused by the Ino mutation prior to bleaching (© Jacob Jorritsma)

Figure 17. Ino Eurasian Collared Dove *Streptopelia decaocto*, juvenile, Ely, Cambridgeshire, England, April 2021; juvenile plumage still unbleached (© Ian Barton)

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hybrid dove carrying the Ino mutation in its genome can introduce the mutation into the population. The gene which harbours the Ino mutation is located on the Z-chromosome (one of the sex-chromosomes). The sex-chromosome carrying the mutation will be passed from one generation to the next, while other characteristics of Barbary Dove become more 'diluted' in each generation, thus the third generation is morphologically identical to a pure Eurasian Collared Dove (see footnote 6). Depending on which species was the male and female parent of the first interspecific hybrid, to the human ear the call will be indistinguishable from Eurasian Collared Dove within five generations (see footnote 6).

In birds, males have two Z-chromosomes and females just one, so only males can possess two different alleles of any gene on the Z-chromosome. These males are heterozygous (i.e. possess two different alleles) for a mutation on the Z-chromosome. The allele for normal (wild) colour is dominant over Ino. Therefore, an Ino offspring is possible from a pair of normal-coloured Eurasian Collared Doves only if the male is heterozygous for the mutation. Ino offspring, however, are always female (van Grouw 2018). Ino males can only be the product of a female with the mutation paired to a heterozygous male. Ino Eurasian Collared Dove females have been recorded breeding but, as the mutation is still very rare in Europe, the chance of pairing with a heterozygous male is tiny. On the Canaries, where the number of Ino-coloured doves is much higher, Ino males are recorded (Fig. 11).

Although the origin of the Ino mutation in European doves is not always certain, in North America there seems little doubt it came from Barbary Dove, rather than recurrent mutation. As already stated, the first birds on the Bahamas escaped from an aviculturist who believed that his Eurasian Collared Doves were Barbary Doves (Smith 1987), so one can assume that at least some of the escapees were hybrids. The fact that throughout the species' current range in North America, from Mexico to Canada, aberrant-coloured Eurasian Collared Doves are recorded rather frequently (Contreras Balderas *et al*. 2011, Rodríguez-Ruíz *et al*. 2017, Hampton 2018), confirms the suggestion that among the founder population at least some carried interspecific genes.

In fact, in North America two different mutations are regularly encountered in Eurasian Collared Dove (Fig. 18), both of which are common in Barbary Dove. One is the aforementioned fawn-coloured Ino mutation (Fig. 19) but the other is a form of leucism, causing white plumage mixed with normal-coloured feathers (Fig. 20). It is a rather odd member of the group of mutations classified as leucism. In leucism white feathers are the result of the congenital and heritable absence of melanin-producing cells from some or all of the skin where they would normally provide the growing feather with melanin. The white pattern in normal leucism occurs already in juvenile plumage and the amount and pattern of white feathering does not change with age. In the form of leucism in Eurasian Collared Dove, however, juvenile plumage is rather different from adult plumage in which the final, static, mix of white and coloured feathers occurs. Instead, juvenile plumage is a mix of white and coloured barbs giving an overall 'grizzled' appearance (Figs. 21–22). Each juvenile feather is replaced by either a fully white or an entirely normal-coloured feather in adult plumage. This form of leucism is rare in birds but occurs in Barbary Dove. In fact, it is the only leucistic mutation present in this species in America, is rather popular among breeders, and is therefore commonly available. The origin of the same mutation in Eurasian Collared Dove in the USA does not therefore appear to be a mystery.

One mutation that certainly occurred in the Eurasian species is Brown (for details of this mutation in birds, see van Grouw 2021) as that mutation is not yet present in Barbary Dove. Brown is probably the commonest mutation in birds in general but remarkably is absent in certain species. It is also one of the first to occur in species bred in captivity and is common in Canary *Serinus canaria*, Budgerigar *Melopsittacus undulatus*, Zebra Finch

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Figure 18. Eurasian Collared Doves *Streptopelia decaocto* showing different mutations (three Ino and one leucistic), Chandler, Arizona, USA, November 2015 (© Theo van Wallene)

Figure 19. Ino Eurasian Collared Dove *Streptopelia decaocto*, Chandler, Arizona, USA, November 2015 (© Theo van Wallene)

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Figure 20. Leucistic Eurasian Collared Doves *Streptopelia decaocto*. (Top) Chandler, Arizona, USA, December 2015; different bird from that in Fig. 21 (© Theo van Wallene); (below) British Columbia, Canada, October 2014 (© John Gordon)

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Figure 21. Leucistic Barbary Dove in full juvenile plumage; the entire feathering is an intermix of white and coloured barbs giving it a 'grizzled' appearance; each feather will be replaced by either a fully white or a normal-coloured feather in adult plumage (Hein van Grouw)

Figure 22. Leucistic Eurasian Collared Dove *Streptopelia decaocto* in partly juvenile plumage, Chandler, Arizona, USA, November 2015; all large wing feathers (primaries, secondaries and tertials) juvenile and still 'grizzled' due to the mix of white and coloured barbs, whereas in adult plumage these feathers are either all white or fully coloured (© Theo van Wallene)

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Taeniopygia castanotis, many European finches (e.g. Common Chaffinch *Fringilla coelebs*, Eurasian Greenfinch *Chloris chloris*, European Goldfinch *Carduelis carduelis*), Japanese Quail *Coturnix japonica*, Muscovy Duck *Cairina moschata*, domestic duck *Anas platyrhynchos* and domestic pigeon *Columba livia*, to name a few. In chickens, which have been domesticated for millennia, the mutation occurred only as recently as 1994 (Carefoot 1996). In Barbary Dove it is unknown, yet. It is also rare in Eurasian Collared Dove, and I am aware of only a few cases.

Brown is, like Ino, caused by a single recessive genetic mutation on the Z-chromosome, and therefore mainly females with this mutation are encountered in the wild. The mutation also causes incomplete melanin synthesis but, in this case, only eumelanin is affected and remains dark brown instead of becoming black. Phaeomelanin is unaffected and therefore a brown Eurasian Collared Dove is more reddish brown than an Ino (Fig. 23). However,

Figure 23. Brown Eurasian Collared Dove *Streptopelia decaocto*, NHMUK 1889.2.2.1516, collected in 1872 in Raipur, India; due to the mutation, incomplete oxidised melanin pigment is very light sensitive and bleaches rapidly, so old plumage can be nearly white, especially parts exposed continuously to sunlight, like the tips of the primaries and central tail feathers. Unlike Ino, in which both eumelanin and phaeomelanin are incompletely oxidised, in Brown eumelanin alone is affected and phaeomelanin is normal, so the plumage of a Brown Eurasian Collared Dove is more reddish brown than an Ino (© Aimee McArdle, Natural History Museum, London)

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Figure 24. Brown female Eurasian Collared Dove *Streptopelia decaocto*, Herk-de-Stad, Belgium, August 2013, with old and strongly bleached plumage (© Jan Ruymen)

incompletely synthesised eumelanin caused by the mutation Brown is very light sensitive and bleaches rapidly in sunlight (Fig. 24). Within a couple of months, fresh, but aberrant, Brown plumage can become nearly white, making correct identification challenging.

Impact of hybridisation

Hybridisation between wild species and their domestic counterparts—feral or free-ranging—is widely considered to threaten biodiversity. Interbreeding may result in the introgression of different alleles, shaped by artificial selection, into wild populations, with potential negative consequences, such as loss of genetic diversity, disruption of adaptation to local conditions or, ultimately, extinction (Rhymer *et al*. 1996, Allendorf *et al*. 2001, Randi 2008). Based on the many papers published on the subject, such concerns appear to be expressed mainly for iconic species like Wolf *Canis lupus* or Wildcat *Felis silvestris*, and species of economic interest such as Red Junglefowl *Gallus gallus*. Such hybridisation should be of equal concern for wild populations of, e.g. Rock Dove *Columba livia* and Mallard *Anas platyrhynchos*, but they do not seem to be on the radar of conservationists. The same applies to Greylag Goose *Anser anser* and its domestic counterpart, where interbreeding may even introduce alleles of another species into wild Greylags. There are two distinct domestic goose lineages, stemming from Greylag Goose and Swan Goose *Anser cygnoides* (Crawford 1990). Only a few original breeds still derive solely from one ancestral species, and most domestic geese are a mix of the two. Any feral 'farmyard goose' interbreeding with wild Greylags will contribute non-specific genes to the population. Even after many generations the influence of Swan Goose on Greylags can be seen in individuals with a visibly darker hindneck. At a molecular level the influence remains much longer, even forever. Its potential impact—negative or positive—on future Greylag populations is unknown (see Heikkinen *et al*. 2020).

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Comparably, many Eurasian Collared Doves show evidence of traits of Barbary Dove in their genome, especially in areas where both species occur or occurred, for example in the Canaries and the USA. Based on the frequency of Ino individuals in other European populations, one can assume that Barbary Dove genes are more widespread than initially assumed. Due to the species' expansion this spread is not unexpected (Currat *et al*. 2008, Quilodran *et al*. 2020).

Discussion

The North American population of Eurasian Collared Doves as a whole can be assumed to be impure. Because many of the founders were probably hybrids (see above), and the first doves to reach mainland Florida interbred with the local feral Barbary Doves (Smith 1987), this assumption seems likely. Further, the high frequency of colour aberrations commonly present in Barbary Dove that also occurs in the American population of Eurasian Collared Doves underlines the suggestion that the founder birds were impure.

Heritable colour morphs can have positive effects in the right habitat, whether they occur naturally in a population or through interbreeding. Coloration *per se* may not directly influence survival, but there is apparently a link between plumage colour and behavioural and physiological characteristics (e.g. greater resistance to stress, more aggression, and different metabolism) associated with survival. Thus, in some cases, colour morphs may behave differently due to their respective physiological properties and eventually, due to differences in behaviour / habitat choice, they may evolve into distinct taxa (van Grouw 2017). As many subspecies of birds in arid areas are often remarkably light coloured, the pale-coloured Ino Eurasian Collared Doves may do well in North American deserts and eventually evolve into a distinct taxon. Indeed, as the genome of all Eurasian Collared Doves in America probably includes some Barbary Dove genes, one may already consider them something other than *S. decaocto*. Over time, when the 'species' becomes well established in North America with several different colour morphs, they may warrant their own taxonomic status. Currently the genus *Streptopelia* includes 17 species (Dickinson & Remsen 2013). The North American Collared Dove might make number 18—deca-octo!

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Appendix 1: How Eurasian Collared Dove got its name

According to an old legend from the Balkans, Eurasian Collared Dove was created by Zeus, god of sky and thunder, to fulfil the prayers of a poor maid. Paid only 18 pieces a year, she prayed to the gods for it to be made known how miserably she was rewarded for her labours by her hard-hearted mistress. Thereupon, Zeus created this dove to proclaim a voluble *deca-octo* [eighteen], which it still does. This story was told to Imre Frivaldszky (1799–1870) by Carl Hinke, who collected the first specimens for the Hungarian Natural History Museum in Budapest (Naumann 1837, Stresemann 1953). Based on this legend, Frivaldszky named the species *decaocto*. In different versions of the same tale Zeus transformed himself or the girl into a dove to proclaim 'eighteen' all over the world to shame the tight-fisted mistress.

Another folklore tale, from Asia Minor, which could be the basis of the dove's name concerns a Roman soldier who took pity on Jesus on his way to Calvary (Stephanides 1957). The soldier wanted to give Jesus some milk but the milkmaid demanded 18 coins. He had only 17 and the seller refused to reduce her price, so when Christ was crucified, because of her meanness she was turned into a dove and condemned to repeat *deca-octo*, eighteen, for the rest of time, to punish and shame her. She would regain her human shape only if she consented to say *deca-epta*, seventeen. In some Balkan countries it was added that if the milkmaid, out of obstinacy, says *deka-ennaea*, nineteen, the world will end!

The message the dove was supposed to give—deca-octo—may not be immediately clear as this two-syllable word does not 'fit' the three-syllable call—*koo-KOO-kook*. However, in several Balkan languages the word eighteen is also a three-syllable word, e.g., *tiz-en-nyolc* (Hungarian) and *opt-spre-zece* (Romanian).

Appendix 2: All the same

Eurasian Collared Doves from the Balkans through Central Asia ('Turkestan') to Korea and Japan are generally larger and paler than Indian birds. Because of this, Hume (1874) described the doves from Yarkand (in the modern Chinese autonomous province of Xinjiang) as a species and stated, 'The Kashgar Ring Dove [Kashgar, in Yarkand; one of the westernmost cities of China] is certainly distinct from the Indian *risorius*'. The specimen he used was collected by Ferdinand Stoliczka in Kashgar on 5 February 1874 (Sharpe 1891) and Hume (1874) therefore named it *Turtur stoliczkae* (Figs. 25–26). For many years *stoliczkae* was often recognised as a subspecies of Eurasian Collared Dove (e.g. Roonwal 1940, Goodwin 1983) based on supposed differences from the nominate, but these are now considered insignificant. Frivaldszky (1838) based his name *decaocto* on doves in the Balkans, so *stoliczkae* of Hume, who evidently was unfamiliar with Frivaldszky's work, is a junior synonym of *decaocto*. The same is true for *torquata* Bogdanow, 1881, from Turkestan, *zarudnyi* Serebrovski, 1927 (Fig. 27), from eastern Iran, and *koreensis* Buturlin, 1934, from Korea, which are all considered junior synonyms of *decaocto*.

Appendix 3: Ino explained

The term 'Ino' (from the Greek or Latin *Ine* = 'belonging to' or 'like') is used in European aviculture for the pale form (sex-linked imperfect albinism) of captive birds such as finches and parrots. Although Ino mutations can be categorised as a form of albinism, they are not albino and many are far from white. The causes of Ino are variations in a gene called SLC45A2 which codes for the protein 'solute carrier family 45 member 2' in melanin cells. Although the precise function of SLC45A2 is unknown, it probably transports molecules necessary for normal melanin synthesis (Domyan *et al*. 2014). Several different mutations (alleles)

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Figure 25. Type specimen of *Turtur stoliczkae*, ZSI 26534, National Zoological Collections of the Zoological Survey of India, Indian Museum, Kolkata, named by Hume (1874) for Ferdinand Stoliczka who collected it on 5 February 1874 in Yarkand. For more than 100 years *stoliczkae* was recognised as a subspecies of Eurasian Collared Dove but is now considered a junior synonym of *decaocto* (© Zoological Survey of India , Kolkata)

Figure 26. Pl. 14 of Hume's *Turtur stoliczkae* in Sharpe (1891) (Hein van Grouw, © Natural History Museum, London)

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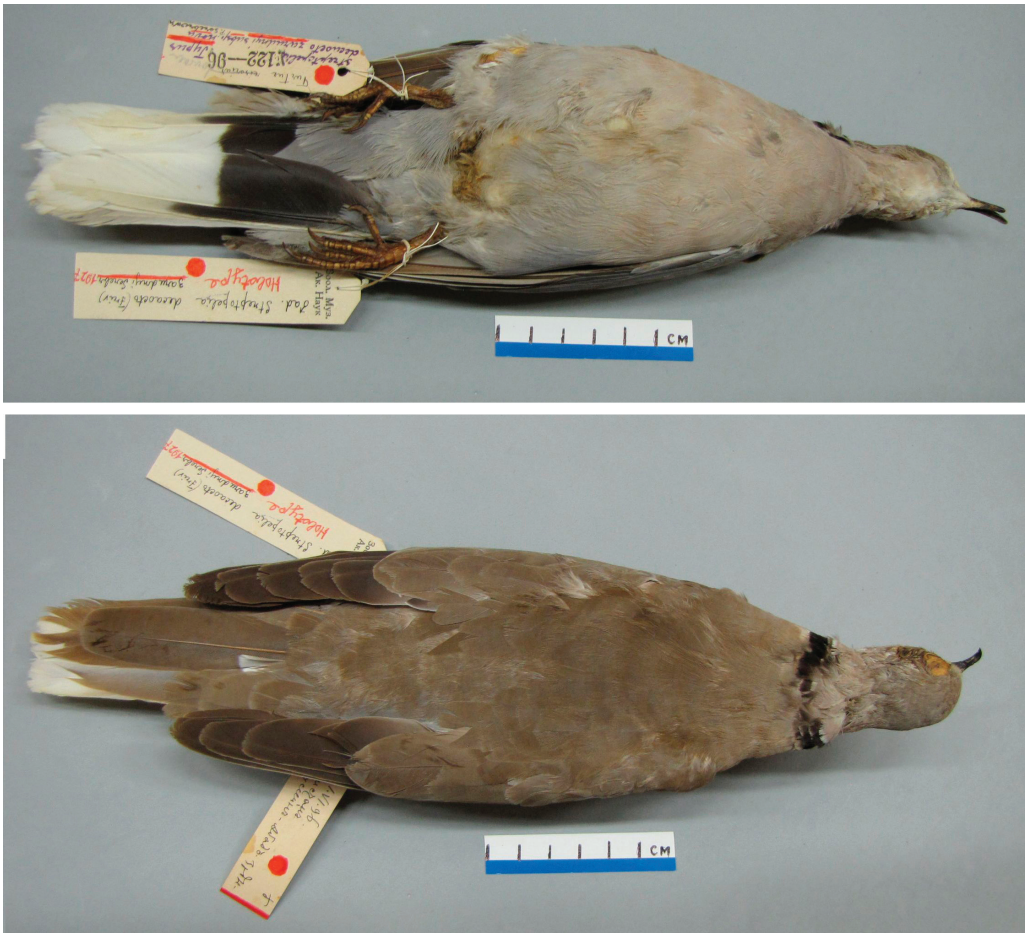

Figure 27. Type specimen of *Streptopelia decaocto zarudnyi*, collected in east Iran on 13 June 1896 by N. Zarudny, ZIN 32107/122-96, Zoological Museum of the Zoological Institute, Russian Academy of Sciences, St Petersburg; the name *zarudnyi* is now a junior synonym of *decaocto* (© ZIN, St Petersburg)

of the SLC45A2 gene, which is located on the Z-chromosome in birds, are known in different species (Gunnarsson *et al*. 2007). These mutations have different effects on the final melanin pigmentation. In some, hardly any melanin is produced, resulting in near-white plumage, whilst in others the plumage is only slightly paler than normal.

The near-white form is often called sex-linked imperfect albinism (Gunnarsson *et al*. 2007) due to its inheritance, and because the plumage is nearly white. In medical science it is known as Oculocutaneous Albinism type 4 (Lamoreux *et al*. 2010). For the darker (less pale) forms, many different names are employed, frequently based on those used in aviculture. I term all mutations of the SLC45A2 gene, Ino.

A common and widespread phenotype in the domestic pigeon, also resulting from a mutation of the SLC45A2 gene, is 'dilution' (Domyan *et al*. 2014, Domyan & Shapiro 2017). Breeding (hybridising) tests conducted by myself and others (Cole & Hollander 1950) have indicated that Ino in Barbary Dove (often also called 'blond' or 'fawn'), and Dilution in the domestic pigeon, are genetically essentially the same, and therefore it can be assumed Ino in Barbary Dove is also the result of variation in the SLC45A2 gene.

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